Coral communities condition in varying wave exposure: the gulf of Cazones, Cuba

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Abstract: Wave exposure can influence community structure and distribution of shallow coral reefs, by affecting organisms both directly and indirectly. To assess the current stony coral community condition under different degrees of wave exposure at a marine protected area of the Gulf of Cazones (SW Cuba), two expeditions were carried out in May 2010 and June 2012. Four sampling sites were sampled at reef crests (1.5 m deep), and twelve at fore-reefs, at 10, 15 and 20 m deep in four geographic locations. Live coral cover, species richness and composition, colony density, and maximum diameter were assessed using the AGRRA 2001 methodology. Multivariate and non-parametric statistics were applied to compare sites. The coral community structure within reef crests was not homogenous. The observed variability of indicators apparently was determined by great coral mortality events resulting from natural disturbances that occurred in the past (hurricanes, bleaching and diseases). Fore-reef coral communities displayed better condition and lower coral mortality than reef crests. Species richness and coral composition varied, while multivariate and statistical methods did not reveal site grouping with regard to wave exposure. The remaining biological condition indicators were similar among sites, except in the most exposed one, where coral cover and coral size were slightly lower. Wave exposure in the gulf of Cazones seemed not to have a significant influence on differences in condition and structure of the assessed coral communities. Rev. Biol. Trop. 64 (1): 78-93. Epub 2016 March 01.

Key words: coral reefs, wave exposure, coral community condition, coral cover, Cuba.

The influence of natural and anthropogenic disturbances on the condition and structure of hard coral communities is one of the fundamental problems in current environmental analyses, because the coral reefs condition has experienced a significant decline in the last decades. There are many studies describing the effect of "natural" acute disturbances like hurricanes on coral reefs (Gardner, Cote´, Gill, Grant & Watkinson, 2005; Álvarez del Castillo, Reyes-Bonilla, Álvarez-Filip, Millet-Encalada & Escobosa-González, 2008; Fisco, 2008; Alcolado, Caballero, & Perera, 2009a). Several papers identify human chronic disturbances such as water pollution (Kuntz, Kline, Sandin, & Rohwer, 2005; Littler, Littler, Brooks, & Lapointe, 2006; McClanahan, Carreiro-Silva, & DiLorenzo, 2007; Lapointe, Langton, Bedford, & Potts, 2010) and sedimentation (Rogers, 1990; Brown, 1997; Torres & Morelock, 2002; Anthony, Ridd, Orpin, Larcombe, & Lough, 2004; Fabricius, De'ath, McCook, Turak, & Williams, 2005; Pandolfi et al., 2005; Lirman & Fong, 2007; Hernández, Sherman, Weil, & Yoshioka, 2009) as driver of coral reef decline.

Natural disturbances from low to moderate intensity, such as chronic wave exposure, are less studied, because their impacts are more difficult to measure due to the wide spatial and temporal scales through which they act upon ecosystems (Langmead & Sheppard, 2004). Evidence suggests that wave exposure influences coral reef dynamic (Geister, 1977). Wave exposure is primarily driven by the fetch (i.e., sea surface area or distance upon wind blows to generate waves), strength and direction of the winds and may influence coral reef dynamics (Chollett & Mumby, 2012; Chollett, Mumby, Müller-Karger, & Hu, 2012). This factor acting with great magnitude can influence the community structure and distribution of corals directly through mechanical stress, by dislodging or breaking them (Denny, 1994), and indirectly through sediment flux (Wolanski, Fabricius, Spagnol, & Brinkman, 2005). Reef sites with relatively high sedimentation rates (induced by waves) have fewer coral species, lower live coral cover and growth rates, greater abundance of branching forms, reduced coral recruitment, decreased calcification, decreased net productivity of corals, and slower rates of reef accretion (Rogers, 1990).

As example of coral reefs with influence of disturbances from variable intensity, we chose the coral communities of the gulf of Cazones (SW Cuba). This area is located within the National Park of Zapata Swamp (Marine Protected Area of Managed Resources declared Biosphere Reserve and Ramsar Site), away from human settlements (towns, tourist facilities, fishing centers) and urban pollution sources. According their geographical position, two types of mechanical disturbances can affect the coral reefs: the chronic exposure to waves, and acute episodic physical disturbance from tropical cyclones. This was verifiable through to remote sensors charts of Chollett et al. (2012).

The goal of this study was to evaluate the structure and condition of coral communities located in sites with variable wave exposition. We asked some questions: Can wave exposure influence biological indicators like live coral cover, density and colony size, and coral composition across a light depth gradient?

MATERIALS AND METHODS

Study area description: The study area is located at the North side within the gulf of Cazones, next to the Peninsula of Zapata, in the South coast of the central part of Cuba (Fig. 1). This gulf is a deep and narrow ocean tongue that enters northward near to the mainland coast ending as a large circular feature better known as "Ensenada de Cazones". The gulf is surrounded by keys and extensive mangrove forests of the mainland swampy coast that attenuates extreme episodes of terrestrial runoff on coral reefs, particularly during the rainy season. According to Pavlidis, Ionin, Ignatov, LLuis-Riera & Avelio (1973), surface currents in the gulf of Cazones moves toward the West driven by the predominant wind pattern from

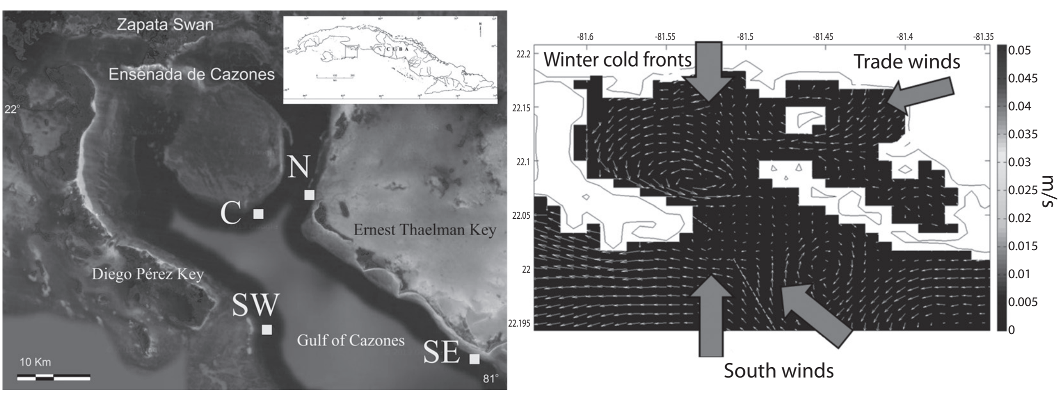

Fig. 1. Map of study area. Left: Geographic location of the gulf of Cazones; right: General trend of winds and surface circulation. Modified scheme from Arriaza et al. (2012). See codes of coral reefs in Table 1.

Northeast-East to West. Inside the West part of the gulf, slow cyclonic circulation pattern is present (Fig. 1). This would drag and circulate the nutrients coming from the swampy coast (Alcolado et al., 2013, according to the circulation model of Arriaza et al., 2012).

Coral reefs in the gulf of Cazones can be classified as fringing reefs (with or without reef crest zones). From the outer borders of the reef crests a flat rocky/sandy zone extends down to 10 m deep. Spur and groove reef systems extend deeper providing more architectural complexity and at 15 to 17 m an abrupt deep fore-reef slope (80°) is present.

Coral reefs in the area have experienced different degrees of wind exposure. Dominant winds include the Trade Winds (from the East and Northeast), Northern winter winds, and sporadic strong "South winds" events (Ballester, 1997). The fetch that influence wave from the North and trade winds on the area is reduced by the land masses. Wave generation by Southwestern winds is reduced given the extension of the very shallow platform of the gulf of Batabanó (Alcolado et al., 2013). Thus, the Southern and Southeastern winds produce waves impact the most these coral reefs. These Southern winds are meteorological events associated to low-pressure centers that move on the Gulf of Mexico (generally between September and May), and they precede the winter cold fronts, sometimes reaching wind speeds of 100 km/h (Ballester, 1997). The gulf of Cazones is also located in a zone sometimes affected by hurricanes and tropical storms (five hurricanes between 1980 and 2010 according to www.noaa.gov).

Survey sites and data analyses: Two expeditions were carried out: in May of 2010 (to evaluate fore-reefs) and June of 2012 to evaluate crest reefs). Four coral reef areas or location sites were chosen with different degrees of wave exposure (Fig. 1) (Table 1). Wave exposure values were obtained from remote sensors charts of Chollett et al. (2012) where the exposure of a location is a function of the shape of the basin, speed and direction of winds. Chollett et al. (2012) measured fetch using the global, self-consistent, hierarchical,

TABLE 1
Geographical location of coral reefs sites, depth and type of habitats

Coral reef (location)	Codes of sites	LN	LW	Depth (m)	Ecological Zone	WE (Ln J / m^{3})	DAH
North (N)	N1	22.1018	81.4901	10	Spur and groove	4.5124	7.0
	N2	22.1018	81.4901	15	Spur and groove	4.5124	7.0
	N3	22.1018	81.4901	20	Fore-reef slope	4.5124	7.0
Central (C)	C1	22.1043	81.5159	1.5	Reef crest	5.4131	7.0
	C2	22.1043	81.5159	10	Spur and groove	5.4131	7.0
	C3	22.1043	81.5159	15	Spur and groove	5.4131	7.0
	C4	22.1043	81.5159	20	Fore-reef slope	5.4131	7.0
Southwest (SW)	SW1	22.0379	81.5173	1.5	Reef crest	5.8528	7.0
	SW2	22.0237	81.5173	1.5	Reef crest	6.0200	7.0
	SW3	22.0266	81.5150	10	Spur and groove	5.8528	7.0
	SW4	22.0266	81.5150	15	Spur and groove	5.8528	7.0
	SW5	22.0266	81.5150	20	Fore-reef slope	5.8528	7.0
Southeast (SE)	SE1	22.0125	81.3417	1.5	Reef crest	6.1615	10.0
	SE2	22.0208	81.3875	10	Spur and groove	5.9768	8.0
	SE3	22.0208	81.3875	15	Spur and groove	5.9768	8.0
	SE4	22.0208	81.3875	20	Fore-reef slope	5.9768	8.0

Values of wave exposition (WE) and danger average of hurricanes (DAH) for the period 1980 at 2008 were calculated according to charts of remote sensors of Chollet et al. (2012).

high-resolution shoreline database (GSHHS version 1.5, Wessel & Smith, 1996), speed and direction of winds were acquired from the QuikSCAT (NASA) satellite scatterometer from 1999 to 2008. The danger average of hurricanes for the period 1980 at 2008 was calculated as the product of the frequency of hurricanes by the intensity average (Saffir-Simpson) according to Chollett et al. (2012) (Table 1).

Four sites were located in reef crest habitat at about 1.5 m deep (except for the N location that lacked zone). The SW location presented two reef crest sites SW1 and SW2 due to the great longitude of the crest. For all four locations, we surveyed coral communities at three depths (10, 15 and 20 m deep, Table 1). Between 14 and 22 replicates benthic 10 m long transects were haphazardly placed at each reef site (Appendix II). Sampling methods applied to indicators were those from AGRRA (2001). Live coral cover was calculated considering the percentages of live tissue intersected by the transect line. Coral colonies larger than 10 cm in diameter that intercepted the transect line, were counted and identified to specie. Maximum diameter of each intercepted colony (observed from above and including the dead parts) was measured. Standing coral colonies with 100 % of mortality were not included in the analysis of coral density and size.

To estimate the variation of biological indicators (live coral cover, density, and maximum diameter) among sites (crest and fore-reefs separately), an analysis of permutational variance (PERMANOVA, Anderson, Gorley, & Clarke, 2008) was performed, using sites as fixed factor for reef crests (one-way factorial design), and locations and depth as fixed factors for fore-reefs (two-way factorial design). The Bray- Curtis similarity index with 999 permutations and 0.05 of significance was applied. A square root transformation was applied to each data matrix.

Differences in coral community structure among sites within reef habitats were analyzed according to coral relative abundance. Species accumulative curves were made, and a non-metric multidimensional ordination analysis (nMDS) was used based on the Bray-Curtis similarity index and the group-average linking method. Only the 95 % of species (in decreasing order) was used in the analysis and was transformed to the square root. The similitude matrix obtained was analyzed by PERMANOVA (999 permutations and 0.05 significance) to determinate statistical variation, using sites as fixed factor for reef crests (one-way factorial design), and locations and depth as fixed factors for fore-reefs (two-way factorial design).

All tests were performed using the PRIMER 6 software and the PERMANOVA version of this program (Anderson et al., 2008). To build graphics the Microsoft Excel 2010 and the Statistica 6.0 programs (StatSoft Inc., 2002) were used.

RESULTS

Live coral cover was significantly different among reef crest sites ($p = 0.001$). The highest live coral cover (62.8 ± 3.9 %, mean ± se) was found at C1, while the lowest at SE1 (14.2 ± 1.8 %) (Fig. 2A). Coral density ($p = 0.047$) had the highest value also in C1 (8.0 ± 0.5 colonies / 10 m) and the lowest at SE1 (5.9 ± 0.7 colonies / 10 m) (Fig. 2B). Mean coral colony maximum diameter in C1 (121 ± 6.1 cm) was significantly higher ($p = 0.001$) than in the remaining reef crest sites (Fig. 2C). See the PERMANOVA complete results in Appendix I, Appendix II, Appendix III and Appendix IV of supporting information.

A total of 14 species of scleractinian corals and one hydrocoral were observed at the reef crest sites. SE1 and C1 sites had the highest number of species (11 species), followed by SW1 and SW2 (Fig. 3A). Among coral species within each site, C1 presented the highest relative abundance (82 %) of *Acropora palmata* (Lamarck, 1816) while *Millepora complanata* (Lamarck, 1816) predominated in SW2 and SW1 (61 % and 53 %, respectively). *Porites astreoides* (Lamarck, 1816) and *M. complanata* predominated in SE1 (36 % and 22 %, respectively). At SE1 we observed that all colonies of *A. palmata* were fully dead standing colonies.

See table of relative abundance of coral per site in Appendix II of supporting information.

The nMDS and PERMANOVA analyses (based on coral relative abundance) showed significant differences among crests with regard to community composition (p = 0.001). Only SW1 and SW2 were similar (Fig. 4). See the PERMANOVA complete results in Appendix I and Appendix IV of supporting information.

Coral indicators in fore-reef sites showed no significant interaction between location and depth through the PERMANOVA analysis (p = 0.715). Total live coral cover average of fore- reef sites was 23 ± 0.5 %. SE1 had the lowest coral cover (20.4 ± 1.8) at 10 m deep (Fig. 2D), while there were not significant differences among sites at 15 m and 20 m in depth. Coral colony density was higher in C2 (9.8 ± 0.7 colonies / 10 m) than in the remaining sites at 10 m, 15 m and 20 m deep (Fig. 2E). The biggest corals were found always in sites of C, while the lowest ones in the sites of

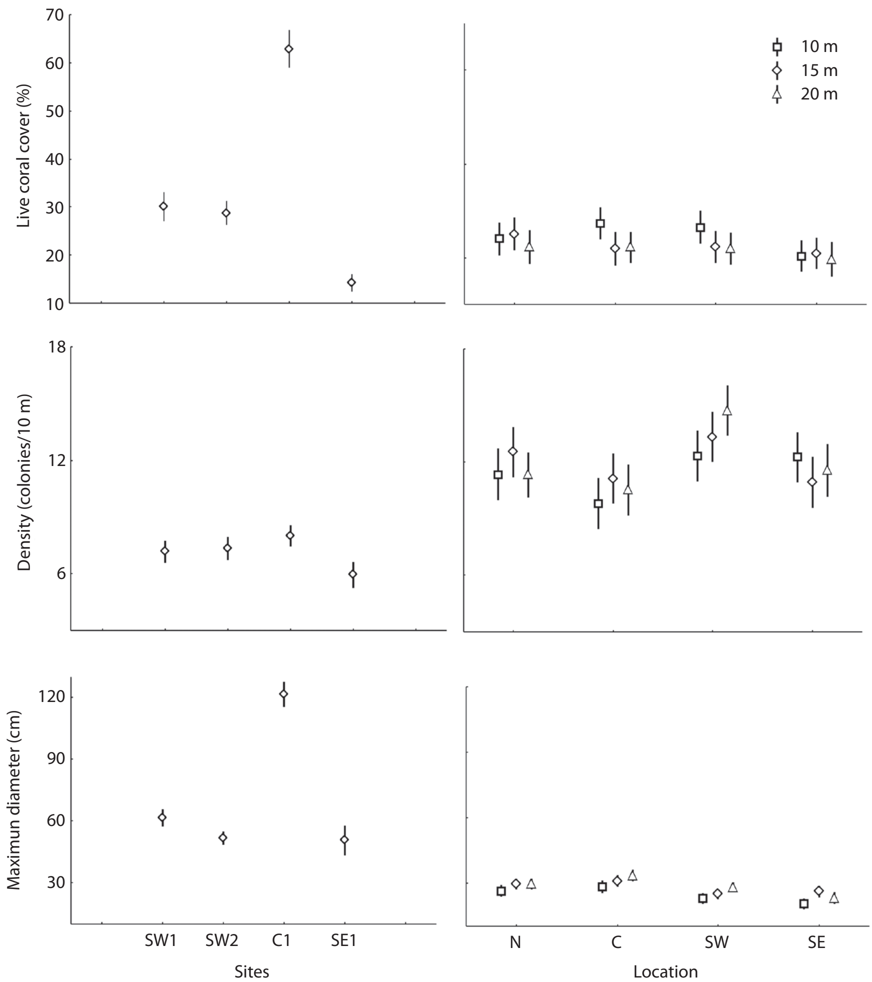

Fig. 2. Coral biological indicators (mean ± standard error). A: Live coral cover in reef crest sites; B: Density in reef crest sites; C: Maximum diameter in reef crest sites; D: Live coral cover in fore-reef sites; B: Density in fore-reef sites; C: Maximum diameter in fore-reef sites. See codes of sites in Table 1.

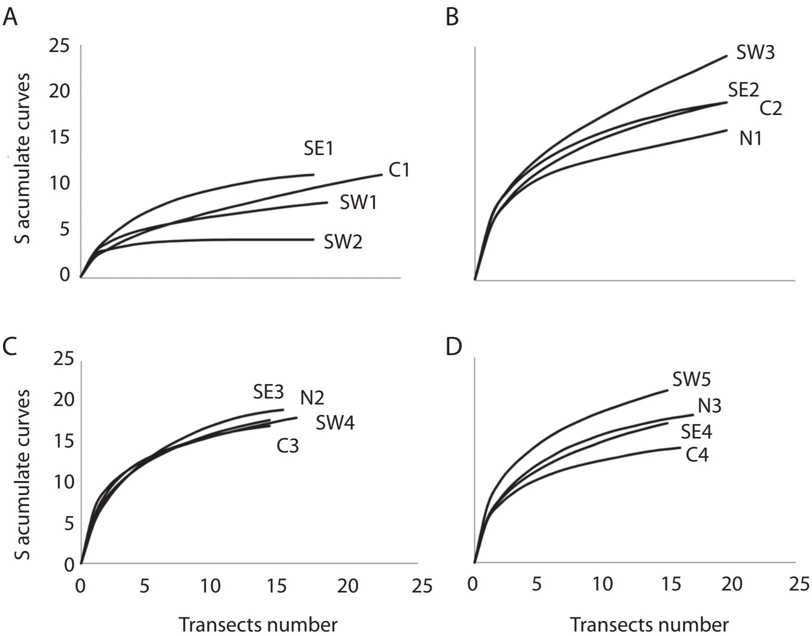

Fig. 3. Result of accumulative curves of number of species (S)/number of transects; A: Crest sites; B: 10m deep sites; C: 15m deep sites and D: 20m deep sites.

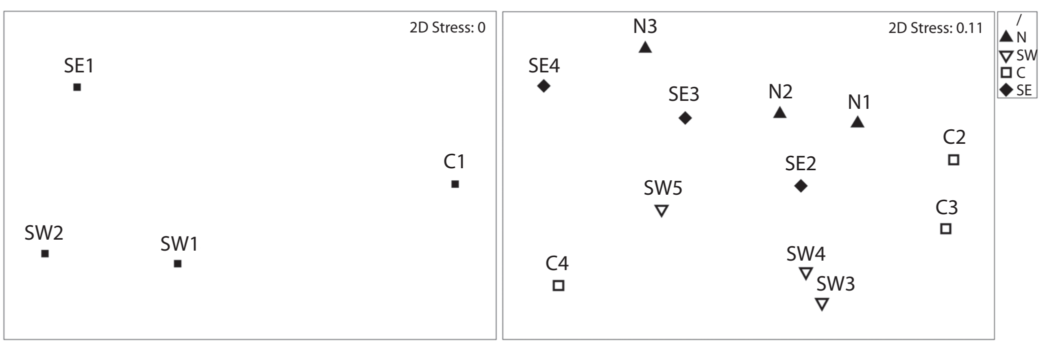

Fig. 4. Results of nMDS analysis. Left: Crest sites; Right: Fore-reefs sites. See codes of sites in Table 1.

SW (Fig. 2F). See the PERMANOVA complete results in Appendix III and Appendix V of supporting information.

At fore-reef sites, coral species richness ranged from 13 (C4) to 23 (SW3). In general, the highest diversity of coral species was found in the fore-reef sites of the SW area. At 10 m deep, the lowest slope of the cumulative species curve was observed in N1; at 15 m deep all species accumulative curves showed similar tendency, and at 20 m deep, the lowest values belonged to C4 (Fig. 3 B, Fig. 3C and Fig. 3D).

The relatively dominant species among corals at the fore-reef 10-15 m deep sites was *Siderastrea siderea* Ellis & Solander, 1786, especially within the N and SE locations. The specie *Orbicella faveolata* Ellis & Solander, 1786 was relatively abundant at the deeper sites, and at C and SW fore-reef sites. Other fairly abundant species were *Agaricia* *agaricites* (Linnaeus, 1758) (SW3 and SW5) and *P. astreoides* (C3 and SE2). *O. annularis* Ellis & Solander, 1786, also showed relatively high percentages at SW2 and SW3. See table of relative abundance of coral per site in Appendix II of supporting information.

The nMDS ordination analysis for the fore-reef zones displayed a dispersed pattern (Fig. 4). The PERMANOVA analysis showed a significant interaction between location and depth for fore-reef sites ($p = 0.001$). The sites at 10 and 20 m deep display significant differences while N2 and SE3 sites at 15 m were similar. See the PERMANOVA complete results in Appendix III and Appendix V of supporting information.

DISCUSSION

At the reefs crests of the gulf of Cazones, the highest values for live coral cover, and colony size were found in the less exposed site (C1). This site had a relatively high dominance of healthy colonies of *A. palmata*, which used to be the main reef-builder coral species of shallow reefs in the Caribbean (Aronson & Precht, 2001; Pandolfi & Jackson, 2001; *Acropora* Biological Review Team, 2005). However, wave exposure does not seem to be the only direct cause of the main differences found among crests. According to Alcolado et al. (2010), in the past decades SW1, SW2 and SE1 had live coral cover and community composition similar to those of C1 today. In 2001, SW1 had live coral cover of 48.5 % in average (Alcolado et al., 2010), with a great number of live colonies of *A. palmata*, many of which were still standing but dead in the present study. It is likely that these reef crests were healthier in the 1980s resembling the typical structure of crest zone of Caribbean shallow reefs described by Geister (1977).

It is possible that the differences in the biological indicators between C1 and the rest of reef crests were apparently a consequence of high coral mortality events that occurred in SW and SE by the end of last century. This suggests that C1 has been more resilient against natural disturbances causing high mortality to *A. palmata*. This species has experienced a significant regional decline as a result of storms, bleaching events, predation and epizootic diseases (Aronson & Precht, 2001; Patterson et al., 2002; Precht, Bruckner, Aronson, & Bruckner, 2002; Rogers & Miller, 2006; Cramer, Jackson, Angioletti, Leonard-Pingel, & Guilderson, 2012; Jackson, Donovan, Cramer, & Lam, 2014).

The mean live coral cover in C1 (~ 60 %) was higher than those reported for other reef crests through the Cuban archipelago, where the “healthiest” reef crests do not exceed 40 %, and a large number of them are less 10 %, revealing a critical state (González-Ferrer et al., 2007, Caballero, Alcolado, & Semidey, 2009; Alcolado et al., 2009b, 2010). Apparently this location has experienced stable conditions for *Acropora* populations. Past studies showed similar cover in 2001, and was approximately 70 %, in the 1980s (Alcolado et al., 2010). Several possible explanations for healthy *Acropora* populations at this site are: (1) a proliferation by asexual reproduction of a few clones genetically resilient to the pathogens affecting the Caribbean; (2) faster recovery by re-growth of surviving colonies; (3) that the pressures affecting the rest of the sub region have not targeted these sites (or colonies) to the same extent (Alcolado et al., 2010); or (4) a greater and faster stabilization opportunity of *A. palmata* branch fragments after storms and hurricanes (Alcolado et al., 2013). The sheltered condition of the C1 should have strongly stimulated coral recovery after extreme events. It should have also significantly favored a higher coral recruitment and survival of young colonies. Another of the most plausible explanation (5) of why this site has more *Acropora* cover is high degree of self-recruitment due to that oceans currents keep coral larvae in that spot. The cyclonic surface water circulation around C1 area could prevent coral gametes and larvae from escaping the area, increasing self-recruitment and concentrate productivity contributing to a higher coral growth and survivorship (Alcolado et al., 2013).

Additionally (6), a higher water fertility and biological richness could provide better condition at C1. Fernández de la Llera, Hidalgo-González, López-García, García-Ramil and Penié-Rodríguez (1990) described a decreasing gradient of concentration of nutrients (N and P) from Zapata swamp to the South of the gulf of Cazones. The proximity of C1 to Zapata swamp and very shallow sheltered lagoons behind of Thaelmann key (both rich in mangrove forests), should have been favorable, considering the provision of non-excessive nutrients that enable greater concentrations of different components of plankton as shown by other researches in the study area (bacterioplankton: Lugioyo, 2003; Lugioyo, Miravet, Pérez, Álvarez, & Espinosa, 2007; phytoplankton: Pérez, Gil, & Loza, 1990; Loza, 2010; microzooplankton: Orozco-Llerena, 1997; fish larvae: Gutiérrez, Montolio, & Frías, 1990; and stage 1 lobster larvae: Alfonso, Frias, Campos, & Baisre, 1991). The plankton should be favoring corals through heterotrophy, making them more resistant (Fabricius, De'ath, McCook, Turak, & Williams, 2005; Schuttenberg & Marshall, 2008) and will be to recover faster.

The worst coral reef crest condition was observed at SE1, but as this site has not been studied before it is not possible to know mortality causes and time of occurrence. It is possible that due to the exposed location of SE1 in the Southern end of the gulf, the destructive effects of hurricanes at the beginning of the century were more intense at this site with no recovery overtime. Storms can be powerful drivers of changes for coral reefs (Álvarez-Filip, Dulvy, Gill, Côté, & Watkinson, 2009), and the effect of hurricanes today may be stronger than in the past (Mumby & Steneck, 2008).

In fore-reefs sites, coral cover, and coral size were slightly lower at SE at 10 m deep. This is the most exposed site studied and wave exposure is expected to be stronger, the sediment suspension to be higher, the slope of the bottom is lower favoring sediment accumulation (Sheppard, 1982). Coral cover was over 20 % at the 10 m deep sites in the locations more exposed to wave (SE and SW). However, lower coral cover has been observed in other Cuban reefs at the same depth under different wave exposure regimes. For example, coral cover at Bajos de Sancho Pardo (NW Cuba) is < 13 %. These reefs are exposed to strong north winds due to cold fronts that create wave exposure average of 7.2 jm/3 (according to Chollet et al., 2012 charts) and have been often affected by tropical storms (Caballero & Alcolado, 2011). Similar conditions are also seen in coral reefs of Santa Lucía (NE Cuba) exposed to fairly constant trade winds with wave exposure average of 7.6 jm/3. At both reefs, average coral cover was below 13 % (Busutil, Caballero, Hidalgo, Alcolado-Prieto, Alcolado, & Martínez-Daranas, 2011; Caballero & Alcolado, 2011). Similarly, coral reefs of Cabo San Antonio, that are exposed to both strong Southern wind events (wave average of 6.7 jm/3) and frequent hurricanes, show a mean coral cover < 10 % at 10 m deep, and their coral communities are comprised of small colonies, mainly of *S. siderea* (Perera, Alcolado, Caballero, de la Guardia, & Cobián, 2013).

In general, the fore-reef sites of the gulf of Cazones displayed bigger live coral cover that others Cuban coral reefs. In our study, mean coral cover for fore-reef sites was 23 %. In contrast, coral cover varied between 8 and 18 % at fore-reef sites from Cayo Coco (NE Cuba) (Clero-Alonso et al., 2006). The weighed national average of live coral cover estimated by Alcolado et al. (2009b) for years 2003-2009 was 13.4 %. Finally, between 2007 and 2010, 74 fore reef sites from Western Cuba presented a mean coral cover of 15.6 % (Caballero, Alcolado, & Semidey, 2009; Caballero & Alcolado, 2011; Perera et al., 2013).

Species richness and coral community composition were not related to wave exposure in fore-reef sites. Coral composition was very variable among locations and depths with no clear grouping in the ordination analysis. Species recognized as resistant to high water turbulence and to sedimentation (*S. siderea*, *P. astreoides*, *M. cavernosa* and *S. intersepta*, according to Herrera & Martínez-Estallela, 1987; Meesters, Bos, & Gast, 1992; Torres &

Morelock, 2002) showed a variable and random relative abundance among sites, being equally abundant in both sheltered and exposed sites.

We concluded that different wave exposure in the gulf of Cazones seems not to have significant influence on the structure and the condition of coral communities. The reef crests were not homogenous. Differences observed are related with the corals health that is associated with previous mortality events. One of the crests has been more resilient that the others. Species richness, coral composition and the other biological indicators did not appear to be fully related to wave exposure in fore-reef, except at 10 m of SE, which is the most exposed site where coral cover and coral size were slightly lower.

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RESUMEN

Condición de comunidades coralinas con diferente exposición al oleaje: El Golfo de Cazones, Cuba. El oleaje es una perturbación natural que puede inferir en la estructura y condición de los arrecifes de coral someros, afectando los organismos directa e indirectamente. Para evaluar la condición de comunidades de corales con diferente exposición al oleaje, se realizaron dos expediciones al Área Marina Protegida del Golfo de Cazones durante mayo 2010 y junio 2012. Se escogieron cuatro arrecifes (localidades) ubicados en posiciones diferentes del golfo. Se ubicaron cuatro sitios en la zona de cresta (1.5 m de profundidad) y 12 en la zona de arrecife frontal (en cuatro localidades a 10, 15 y 20 m de profundidad) donde se replicaron transectos lineales (10 m de largo) de muestreo. Se evaluó la cobertura de coral vivo, riqueza y composición por especies, densidad y diámetro máximo de las colonias mediante la metodología AGRRA 2001. Para la comparación entre sitios se aplicaron métodos evaluativos multivariados y análisis estadísticos no paramétricos. La estructura y condición de la comunidad de corales en las crestas fue distinta pero la variabilidad observada parece responder a grandes eventos de mortalidad producto de huracanes, blanqueamientos y enfermedades del pasado. La condición de los arrecifes frontales fue más favorable observándose menor mortalidad coralina. La riqueza y composición por especies fue variable y los métodos estadísticos y multivariados no definieron grupos de sitios con similitud respecto a la exposición al oleaje. Los demás indicadores biológicos de condición fueron parecidos entre sitios, excepto en el más expuesto al oleaje, donde la cobertura y la talla de los corales fueron ligeramente inferiores. En general, la diferente influencia del oleaje dentro del golfo de Cazones, parece no afectar significativamente la estructura y condición de las comunidades coralinas.

Palabras claves: arrecifes de coral, exposición al oleaje, comunidades coralinas, cobertura de coral, Cuba.

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APPENDIX I

Results of the permutational multivariate analysis of variance (PERMANOVA) based on the Bray-Curtis dissimilarity index for coral parameters at crest-reefs sites

Indicator	PERMANOVA table of results						
	Source	df	SS	MS	Pseudo-F	P(perm)	perms
Coral cover	Sites	3	11 586	3 862	27.438	0.001	998
	Res	67	9 430.6	140.76			
	Total	70	21 017				
Coral density	Sites	3	857.08	285.69	2.6455	0.047	999
	Res	70	7 559.3	107.99			
	Total	73	8 416.4				
Maximun diameter	Sites	3	42 962	14 321	56.722	0.001	998
	Res	525	132 550	252.47			
	Total	528	175 510				
Coral relative abundance	Sites	3	91 184	30 395	28.625	0.001	999
	Res	70	74 329	1 061.8			
	Total	73	165 510				

APPENDIX II

Relative abundance (%) of corals by site

Ecological zone	Crest				Fore-reefs											
Depths (m)	1.5	1.5	1.5	1.5	10	15	20	10	15	20	10	15	20	10	15	20
	Sites															
Species	SW1	SW2	C1	SE1	N1	N2	N3	SW3	SW4	SW5	C2	C3	C4	SE2	SE3	SE4
Siderastraea siderea	0.0	0.0	1.0	11.6	35.2	36.7	36.4	19.8	18.9	8.2	31.7	13.7	23.5	25.7	39.1	29.1
Porites astreoides	13.7	27.1	3.8	36.2	8.9	6.0	1.4	9.8	16.0	5.7	19.5	20.5	3.6	14.6	5.0	5.5
Orbicella faveolata	0.0	0.0	1.1	0.0	14.3	20.4	20.4	6.5	9.9	17.9	7.4	14.7	29.9	13.4	12.6	15.5
Agaricia agaricites	0.0	0.0	0.0	0.0	5.8	4.5	7.8	24.2	17.3	28.2	4.5	6.0	12.2	12.4	9.8	14.8
Millepora complanata	53.0	61.5	8.1	22.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acropora palmata	15.9	5.4	82.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stephanocoenia intercepta	0.0	0.0	0.0	0.0	9.9	11.2	6.5	3.7	2.8	10.2	1.4	6.5	1.1	7.6	13.2	18.2
Orbicella annularis	2.5	0.0	0.7	6.0	4.6	4.3	1.8	13.5	14.1	5.6	5.8	7.0	4.7	3.8	1.0	0.0
Porites furcata	12.0	6.1	0.6	2.5	3.2	0.0	0.0	0.9	2.3	1.0	7.4	7.8	0.0	5.1	1.1	0.0
Porites porites	0.0	0.0	0.0	11.9	6.0	3.1	0.8	3.0	6.4	1.7	4.5	5.5	1.1	1.0	2.0	0.0
Agaricia lamarcki	0.0	0.0	0.0	0.0	0.0	0.4	8.4	1.3	1.8	8.6	0.0	0.0	11.3	0.8	3.9	5.4
Montastraea cavernosa	0.0	0.0	0.0	0.0	5.1	3.7	1.9	4.2	3.2	3.1	7.9	1.2	0.0	3.6	1.1	0.9
No. of transects	18	17	22	18	15	15	16	15	14	16	15	16	15	15	15	15

Only 95 % of species counted at crest and fore-reefs sites is represented. See codes of sites in Table 1.

APPENDIX III

Results of the permutational multivariate analysis of variance (PERMANOVA) based on the Bray-Curtis dissimilarity index for biological trait data of fore-reefs sites

Indicator	PERMANOVA table of results						
	Source	df	SS	MS	Pseudo-F	P(perm)	perms
Coral cover	Location	3	588.62	196.21	3.8105	0.010	999
	Depth	2	304.64	152.32	2.9582	0.046	997
	Location x depth	6	197.87	32.978	0.6405	0.715	999
	Res	165	8 496	51.491			
	Total	176	9 575.9				
Coral density	Location	3	949.81	316.6	8.9117	0.001	999
	Depth	2	62.058	31.029	0.8734	0.409	999
	Location x depth	6	288.37	48.062	1.3528	0.232	999
	Res	170	6039.6	35.527			
	Total	181	7 337.9				
Maximun diameter	Location	3	53 858	17 953	26.785	0.001	998
	Depth	2	11 902	5 951.2	8.8793	0.001	999
	Location x depth	6	5 357.1	892.86	1.3322	0.200	999
	Res	2 149	1 440 300	670.24			
	Total	2 160	1 513 600				
Coral relative abundance	Location	3	35 941	11 980	11.258	0.001	999
	Depth	2	26 738	13 369	12.562	0.001	998
	Location x depth	6	17 496	2 916.1	2.7401	0.001	998
	Res	171	181 980	1 064.2			
	Total	182	262 000				

APPENDIX IV
Results of Pair-Wise Tests (PERMANOVA) of coral parameters at crest-reefs sites

Indicator	Groups	t	P (perm)	perms
Coral cover	SW1. SW2	0.220	0.888	998
	SW1. C1	5.985	0.001	997
	SW1. SE1	3.455	0.001	998
	SW2. C1	6.888	0.001	998
	SW2. SE1	3.627	0.001	998
	C1. SE1	7.625	0.001	999
Coral density	SW1. SW2	0.975	0.339	693
	SW1. C1	0.550	0.600	897
	SW1. SE1	0.409	0.722	828
	SW2. C1	1.407	0.160	943
	SW2. SE1	0.486	0.672	896
	C1. SE1	0.758	0.435	985
Maximun diameter	SW1. SW2	1.630	0.084	997
	SW1. C1	5.767	0.001	998
	SW1. SE1	2.047	0.030	998
	SW2. C1	6.802	0.001	999
	SW2. SE1	2.086	0.032	998
	C1. SE1	4.333	0.001	999
Coral relative abundance	SW1. SW2	1.1714	0.278	998
	SW1. C1	7.1125	0.001	999
	SW1. SE1	3.2597	0.001	997
	SW2. C1	10.732	0.001	998
	SW2. SE1	3.0614	0.001	999
	C1. SE1	6.4779	0.001	999

See codes of sites in Table 1.

APPENDIX V

Results of Pair-Wise Tests (PERMANOVA) of coral parameters at fore-reefs sites

Indicator	Depth Groups	10 m			15 m			20 m		
		t	P(perm)	perms	t	P(perm)	perms	t	P(perm)	perms
Coral cover	N. C	1.529	0.149	997	0.746	0.463	997	0.260	0.857	998
	N. SW	0.840	0.436	999	0.886	0.393	998	0.468	0.718	997
	N. SE	2.014	0.058	998	1.063	0.280	997	1.056	0.323	999
	C. SW	0.599	0.597	999	0.549	0.596	997	0.260	0.849	999
	C. SE	2.995	0.004	998	0.674	0.522	999	1.397	0.179	999
	W. SE	2.087	0.038	998	1.269	0.191	997	1.572	0.115	991
Coral density	N. C	2.065	0.040	904	1.294	0.207	910	0.663	0.594	948
	N. SW	1.087	0.305	837	1.153	0.251	896	3.270	0.003	979
	N. SE	0.760	0.446	950	1.437	0.154	934	0.285	0.850	979
	C. SW	2.545	0.017	917	2.831	0.010	809	3.522	0.001	861
	C. SE	1.983	0.056	936	0.232	0.861	832	0.769	0.502	903
	W. SE	0.365	0.739	903	2.891	0.007	786	2.572	0.019	958
Maximun diameter	N. C	1.230	0.230	999	0.330	0.889	998	2.640	0.004	999
	N. SW	2.528	0.005	998	2.783	0.002	997	1.336	0.171	999
	N. SE	4.186	0.001	997	2.845	0.004	999	3.934	0.001	998
	C. SW	3.638	0.001	998	2.538	0.003	999	3.956	0.001	998
	C. SE	5.302	0.001	998	2.622	0.008	999	6.524	0.001	998
	W. SE	1.564	0.104	998	0.766	0.486	997	2.668	0.005	999
Coral relative abundance	N. C	1.628	0.017	999	2.346	0.001	999	1.727	0.016	998
	N. SW	2.464	0.001	999	2.360	0.001	998	2.092	0.001	999
	N. SE	1.612	0.011	999	0.821	0.671	998	1.212	0.189	999
	C. SW	2.061	0.001	999	1.837	0.002	999	1.878	0.001	998
	C. SE	1.622	0.018	998	2.490	0.001	999	2.170	0.001	998
	W. SE	1.770	0.001	999	2.472	0.001	999	1.768	0.002	998

See codes of location in Table 1.